

**ENERGETICS CONSEQUENCES OF CHASE BY TUNA PURSE-SEINERS
FOR SPOTTED DOLPHINS (*STENELLA ATTENUATA*)
IN THE EASTERN TROPICAL PACIFIC OCEAN**

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ABSTRACT

Daily energy costs and mass-specific power outputs were estimated for un-associated *Stenella attenuata* ranging in size from neonate through adult under normal (non-chase) conditions and for conditions including 1 chase of 15, 30, or 60 minutes with swimming velocity ranging from 0.25 to 7.5 meters/second. Daily costs and mass-specific power outputs were also estimated for drafting mother-calf pairs under conditions of gliding drafting or full drag gliding. At the most likely chase reaction speed of about 3 m/second and chase duration of 30 minutes, estimated increase in daily caloric cost ranged from about 12% in neonates to about 6% in adults. Estimated cost increases were halved for 15 minute chases and doubled for 60 minute chases. The relative infrequency of chase (about on the order of 8 times per year) implies that chases probably do not cause a significant long-term adverse impact on daily energy costs for *Stenella attenuata* in the ETP.

In contrast, estimated mass-specific power outputs indicate that size-specific power production capacity likely significantly limits the ability of non-drafting *Stenella* calves to maintain speed with adult dolphins in a school fleeing tuna vessel speedboats during chase. Due to observed decreases in fraction of total body mass composed of propulsive muscle with decreasing body size, as well as simple decreases in total body size with decreasing age, neonate dolphins for example apparently must expend about 4.6 times the power as an adult, to maintain the same speed. Even two-year old calves likely require about 1.5 times the power needed by an adult, to maintain any given speed. As a result, the duration of time over which *Stenella attenuata* of various sizes can maintain any given speed decreases rapidly with body size. For example, for sustained swimming throughout durations likely experienced during chases by tuna vessel speedboats, i.e., on the order of several to many minutes, adult *Stenella* are likely capable of maintaining velocities of about 3 m/second but neonates are likely able to sustain speeds of only about 1.7 m/second for that duration of time.

Neonates and young calves could presumably avoid falling behind by drafting on their mothers. This would not appear to place much additional energetic burden on the mother because estimated energy costs for gliding drafting add only about 7 to 10% to the mother's estimated individual energy costs. The added drag would slow the mother eventually but the effect would likely not be significant for chases less than about 30 minutes duration. However, it is not likely that drafting can be maintained during the relatively high speeds characteristic of response to chases by tuna vessel speedboats. This is a problem because mother dolphins in a flight reaction to chase are likely to be more motivated to stay with the rest of the school than to slow down to accommodate their calves. Thus, it appears very likely that the smaller the calf and the longer the chase, the more likely the calf will be left behind. In addition, the longer the separation, the higher the likelihood of predation mortality to the calf.

Tuna vessels should avoid chases of schools with calves, minimize chase durations, and also minimize the total time of set, in order to minimize chase-related calf mortality.

INTRODUCTION

Tuna purse-seiners in the eastern tropical Pacific Ocean catch schools of large yellowfin tuna by locating, chasing and encircling schools of dolphins with which the tuna frequently associate in

this area (NRCCRPM 1992). Although the massive dolphin mortality that used to be associated with this fishing method appears to have been largely eliminated (IATTC Reports), concern continues that the chase procedure is causing significant harm to the dolphins both directly in terms of set-related unobserved mortality, especially of calves (Archer et al. 2001), and indirectly in terms of adverse capture-stress effects on reproduction and/or survival rates of the affected dolphin stocks (Curry 1999, Donahue 2000).

One unavoidable consequence of the chase procedure is an additional energetics burden imposed on the dolphins as they interrupt their normal activities to flee during the chase, wait in the net during the pursing procedure, and then flee the net during the backdown procedure that releases the dolphins prior to bringing the tuna to the boat for loading. These activities will result in increased cost of swimming during the chase phase and release phase, overall increased metabolism due to stress responses during all phases, and interruption of normal feeding patterns during the event and during recovery in its aftermath. Of these energy-related reactions to chase and encirclement, the increased cost of swimming is likely to far outweigh the other factors due to the remarkably fast increase in power requirements that accrues to swimmers with increasing velocity¹. Thus, estimating the potential energy costs of chase may provide fruitful insights into unobserved effects of chase and encirclement on ETP dolphins.

In order to examine these potential energy costs, the present study adapts for ETP dolphins a standard hydrodynamics model of swimming cost for tunas (i.e., carangiform form of locomotion with semilunate lunate tail (e.g., Webb 1975, Magnuson 1978) in order to estimate cost of swimming for dolphins of various sizes traveling at various velocities during an average chase duration of 30 minutes (Perkins and Edwards 1998), as well as for chases of 15 and 60 minutes duration for comparison. Because mothers with dependent young, particularly neonates and infants less than a year old, are likely to be the most severely challenged component of a chased school (Edwards 2001), the study includes estimates of the potential effects of chase on mother-calf energetics, especially with respect to the habit of drafting whereby very young (small) dolphins appear to move effortlessly alongside the mother (or other large adult) in some sort of hydrodynamic “free ride” (e.g., Norris and Prescott 1961). Model results are discussed in relation to the expected effects of a single chase during a single day, with some additional discussion of the potential effects over longer time periods (e.g., months or years). Readers of this study should remain aware that the model

¹*Drag* on an object moving through the water increases as the square of velocity, e.g., doubling the speed incurs a quadrupling of drag forces to be overcome (e.g., Hoerner 1958, Vogel 1981, eq. 5.4). Worse, the *power* required to overcome that increased drag increases at the cube of velocity (because power = force*velocity, where here the force is hydrodynamic drag, e.g. Alexander 1999 quoting Videler 1993), so that a dolphin doubling its speed increases its power requirements by a factor of 8 (e.g., Weihs and Webb 1983, Table 11-1).

results presented here are *estimates* of energy costs, although the word “estimate” may not appear in all cases (e.g., in titles of figures).

An independent scientific peer review of this work was administered by the Center for Independent Experts located at the University of Miami. Responses to reviewer’s comments can be found in Appendix A.

METHODS

Data Sources. Model results were calculated for 8 individual *Stenella attenuata* ranging in size (age) from newborn through adult. Size increase intervals were selected to emphasize changes during the early months (Table 1). Size at age up to two years old was estimated from Hohn and Hammond (1985). Size of adult reproductive female was estimated from Perrin et al. (1976). Estimated wet weight (Figure 1), estimated wetted surface area including fins (Figure 2), percent added surface area due to fins (Figure 3), estimated maximum body diameter (Figure 4) and estimated fraction of total body weight composed of propulsive musculature (Figure 5) were derived from measurements of *Stenella attenuata* captured in the ETP. Planar area of fins was increased by 6% to account for curvature of the fins, based on measurements of individual slices from fins and flukes from 1 small and 1 large dolphin, 132 cm and 193 cm in length respectively.

Model selection. The energetics model used here to estimate cost of swimming by *Stenella attenuata* in the ETP is essentially the same as found in Edwards (1992), with the exceptions that 1) new data were used to estimate body parameters and 2) the estimate of fin and induced drag was replaced by the multiplier 3 (details to follow). The model uses standard hydrodynamics equations and methods (e.g., Hoerner 1965, Hertel 1969, Webb 1975) to estimate hydrodynamic drag on a steadily moving fully submerged streamlined body of revolution in turbulent flow with body surface area increased to specifically include the surface area of fins and flukes², and with drag estimates increased to account for body and fin movements. Because energy to move forward (thrust energy) must exactly balance the drag experienced by a swimming animal, estimating total drag energy is equivalent to estimating thrust energy (e.g., Fish and Rohr 1999), i.e., energy cost to swim.

Although the drag-based model used here depends on many assumptions and simplifications, it is the best tool currently available with which to estimate swimming energetics of *Stenella attenuata* in the ETP. More direct estimation methods would be preferable, but direct observation of swimming by neonate through adult *Stenella* is not currently feasible. There are no *Stenella* of any age or size currently available for study in captive situations, nor are there any practical ways to collect swimming data via direct observation of *Stenella in situ* in the ETP. The two most popular alternative methods of estimating energy cost of swimming (estimation of gliding drag during deceleration (e.g., Skrovan et al. 1999) and estimation of thrust production during steady horizontal swimming (e.g., Fish 1993, 1998)) both depend upon video films of actively swimming dolphins in order to provide the parameter estimates required for the calculations of drag or thrust. The third alternative - direct measurement of oxygen consumption (or perhaps heart rate, if a heart rate - O₂

²Frank Fish, University of Pennsylvania, pers. comm,

consumption calibration could be achieved) of various sizes of *Stenella* swimming at various speeds for various durations, with and without chase, including mother-calf pairs, is also logistically out of the question.

Though the model used here is not perfect, its credibility can be assessed to some extent by comparing model results with existing reports of energy costs for swimming dolphins from other studies. In the results section, comparisons will be made to the extent possible between model estimates presented here and results presented in these other studies.

Because energy costs have not been measured directly for living dolphins swimming at *sustained* speeds faster than about 3 m/second (although many estimates exist of short-term power outputs during maximum and/or burst effort, Table 2) model estimates are the only available recourse for estimating power requirements at these higher speeds. The best that can be done is to incorporate to the extent possible, existing information and data into the model formulation and then to compare the model results with existing data where such comparisons are possible. Direct verification of model results will have to wait until methods are developed to accurately measure energy costs at the higher velocities and in freely swimming *Stenella* in the ETP.

Model formulation. In order to better understand the effect that one chase by a tuna vessel during a 24-hour period may have on total daily energy cost to dolphins of different sizes, standard (basal) metabolism (STD) was also estimated for each dolphin as function of wet weight. The relationship used here to estimate STD as function of size follows Heusner (1982) for reasons detailed in Edwards (1992). This formulation is particularly appropriate for the current modeling exercise because it predicts relatively higher basal metabolism in younger animals, consistent with observations from a variety of homeotherms (e.g., Brody 1945, Blaxter 1989). Energy expended in specific dynamic action and in fecal and urinary losses were not included in the daily cost estimates because these are relatively small compared to active and standard metabolism, they are proportionally similar across all sizes, they are independent of swimming velocity, and therefore they would not contribute much to understanding size-related effects on *Stenella* due to chases of various velocities and durations.

STD (in calories per day) was estimated here as daily caloric cost where

$$\text{STD} = S_a * \text{wwg}^{S_b}$$

with $S_a = 1380$, $S_b = 0.67$, and wwg is total dolphin body wet weight in grams (Edwards 1992).

Total thrust power (PWR; in watts) required of a dolphin of a given total length (rostrum to fluke notch) to overcome hydrodynamic drag while swimming fully submerged (Hertel 1969) at a given velocity was estimated as

$$\text{PWR} = \text{MP}/(\text{ME}*\text{PE})$$

where MP (in watts) is mechanical power required to overcome hydrodynamic drag, ME is muscle

efficiency³, and PE is “propeller efficiency” (efficiency of propulsion by flukes)⁴. MP was estimated as a function of total hydrodynamic drag (Dt; in dynes) and velocity (VL; in cm/sec) as

$$MP = (Dt*VL)/(10^7)$$

where the factor 10^7 converts (Dt*VL) to watts. The cubic relationship between velocity and thrust power (to overcome drag) is supported by observations of swimming kinematics of *Tursiops truncatus* swimming between 1 and 6 m/sec (power = $f(VL^{2.91})$, Fish 1993).

Total drag was estimated as function of drag due to body, fins and movements of body parts as

$$Dt = 0.5*N*(VL^2)*Sw*Ct*3$$

where N = density of seawater (1.025g/cm^3), Sw is wetted surface area of the body and Ct is coefficient of total drag. The factor 3 accounts for the increase over gliding drag caused by body movements during swimming⁵. The squared relationship between velocity and total drag is supported by the observed relationship between total drag and velocity in free swimming *Tursiops truncatus* (Skrovan et al. 1999, equation 6).

Sw (in cm^2) was estimated as

$$Sw = Sa*(TL^{Sb})$$

where TL is total length (in cm) and Sa = 0.2993 and Sb = 2.05 based on a sample of 19 *Stenella attenuata* from the ETP ranging in size from 71-201 cm TL (Figure 2). Sw includes surface areas of fins and flukes in addition to body surface area.

Ct was estimated from the formula for drag of submerged (i.e., greater than 3 body diameters

³ME = 0.2 based on studies of muscle efficiencies in terrestrial animals (e.g., Goldspink 1977), man (Alexander 1983, quoting Dickinson 1929) and dolphins (Fish 1993, 1996).

⁴PE = 0.85 based on studies by Fish (1998), also Webb 1975, and Yates 1983.

⁵Based on studies of gliding vs. actively swimming dolphins (Skrovan et al. 1999 and references therein).

below the surface (Hertel 1969)) streamlined bodies of revolution moving at constant velocity (e.g., Hoerner 1965, Webb 1975) as

$$C_t = C_f * [1 + (1.5 * (D_a / TL)^{3/2}) + 7 * (D_m / TL)^3]$$

C_f is the coefficient of friction drag and D_m (in cm) is maximum body diameter where

$$D_m = D_a * TL^{D_b}$$

where $D_a = 0.12$ and $D_b = 1.065$ based on measurements from a sample of 24 *Stenella attenuata* from the ETP ranging from 71 to 201 cm TL (Figure 4).

C_f was estimated from the formula for submerged streamlined bodies revolution moving at constant velocity in turbulent flow (e.g., Webb 1975) as

$$C_f = 0.072 * RL^{-0.2}$$

where RL is Reynold's number, estimated here as

$$RL = (TL * VL) / \nu$$

where ν is kinematic viscosity (= 0.01 Stokes) assuming turbulent flow at the boundary layer (Lang and Daybell 1963, Videler and Kam. 1985, Fish and Hui 1991, Fish 1993))

For un-associated dolphins in this model, velocity was assumed to be either a particular chosen chase velocity (when estimating the cost of chase) or the optimum velocity for dolphins of given sizes (when estimating non-chase costs). Optimum velocity (V_{opt} ; in cm/sec) was estimated as

$$V_{opt} = VL_a * TL^{VL_b}$$

where $VL_a = 20.6$ and $VL_b = 0.43$ assuming velocity scales with length in ETP *Stenella attenuata* in the same manner as for ETP yellowfin tuna (*Thunnus albacares*). As geometrically similar swimmers, hydrodynamic constraints should be the approximately the same for both animals (Edwards 1992). This formulation predicts V_{opt} of about 168 cm/second for adult *Stenella* 190 cm TL, which corresponds well with the observed preferred routine swimming speed of 1.6 m/second in 2 morphologically similar *Delphinus delphis* in captivity (173 and 175 cm TL, 60 and 55 kg, Hui 1987).

The calculations above generate estimates of the power required per unit time for a dolphin of a given size to swim at a given velocity, in watts (joules/second). The next step in the modeling process is to estimate the total cost of swimming for a given dolphin at a given velocity for a given duration of time at that speed, i.e., to estimate the work involved.

Swimming work during chase periods at a particular velocity was estimated as

$$W_{cj} = PWR_c * T_c$$

where W_c (in joules) is work expended during chase, PWR_c is power (in watts, i.e., joules/sec) required to swim at a given chase speed and T_c (in seconds) is duration of chase. Cost of chase in joules was then converted to calories/chase (W_{cc}) as

$$W_{cc} = W_c/4.184.$$

Swimming work (in joules) during non-chase periods (i.e., while swimming at V_{opt} if unassociated or at V_{opt} for adult if associated) was estimated as

$$W_o = PWR_o * T_o$$

where W_o = work expended while swimming at V_{opt} (in joules), PWR_o is power required to swim at V_{opt} (in watts, i.e., joules/sec), and T_o (in seconds) is time spent swimming at V_{opt} .

Conversions from watts to calories/day at V_{opt} was accomplished by multiplying watts by 20650 (i.e., 60 seconds*60 minutes*24 hours/(4.184 joules/calorie)).

Watts/kg (in wet weight; ww_{kg}) was estimated as for a given velocity as

$$\text{watts/kg} = PWR/ww_{kg}$$

Watts/kg was estimated two ways, first using total body wet weight and second using wet weight of propulsive muscle only. Total body wet weight (ww_{bkg} , in kg) was estimated from total length (in cm) as

$$ww_{bkg} = TL_a * TL^{TL_b}$$

with $TL_a = 1.19E-05$ and $TL_b = 2.97$ based In-In regression of data from a sample of 23 *Stenella attenuata* from the ETP ranging in size from 71 to 201 cm TL (Figure 1). Wet weight of propulsive muscle (ww_{mkg} , in kg) was estimated from weight weight (in kg) as

$$ww_{mkg} = WW_{ba} * ww_{bkg}^{WW_{bb}}$$

with $WW_{ba} = -2.3$ and $WW_{bb} = 0.27$ based on regression of data from a sample of 16 *Stenella attenuata* from the ETP ranging in size from 71 to 199 cm TL (Figure 5). Propulsive muscle was assumed to include all muscle posterior to the front insertion of the dorsal fin, in order to include the entire tail musculature plus insertion areas.

All morphological data and relationships presented here were collected by dissection of dolphins killed during tuna purse-seine operations and subsequently transported frozen from the ETP to the NMFS lab in La Jolla, CA.

Un-associated dolphins. Energy costs of swimming while un-associated were estimated for each of the 8 simulated individual *Stenella* over a range of chase speeds and durations (Table 1). The range

of estimated swimming speeds during chase is unrealistically wide (from 0.25 to 7.5 m/sec) in order to provide a full picture of energy costs that can be confidently assumed to encompass the true range of swimming speeds performed by *Stenella attenuata* in response to chase by tuna boats in the ETP. Chase durations of 15, 30, and 60 minutes were selected to encompass the majority of chase durations reported by scientific observers on tuna vessels in the ETP, with the majority of chases lasting approximately 30 minutes (Myrick and Perkins 1995).

Daily energy costs *without chase* were estimated as the sum of standard plus active (swimming) metabolism, where energy cost of active metabolism was estimated assuming travel for 24 hours at length-specific V_{opt} . Daily energy costs for a day *including 1 chase* was estimated as the sum of standard and active metabolism, where the cost of swimming at V_{opt} for a given chase duration was replaced with the estimated cost of swimming at the given chase velocity for the given chase duration (e.g., for a day with 1 30-minute chase, dolphins were assumed to swim their length-specific V_{opt} for 23.5 hours, and at the chase velocity for 30 minutes. The total daily cost of swimming was then the sum of the V_{opt} cost for 23.5 hours plus the chase cost for 30 minutes).

The formulae described above were used to estimate, for each size of *unassociated* dolphin, a variety of measures of absolute energy costs for active metabolism incurred by *Stenella* as a function of animal size, swimming velocity, and chase duration. These measures included hydrodynamic drag (dynes), cost of transport ($J\ kg^{-1}\ m^{-1}$), thrust (drag) power (watts), total metabolic power (watts), and mass-specific power output by total body (watts/kg body) and by propulsive muscle (watts/kg propulsive muscle), and calories and joules expended during 1 60-minute chase. The estimates of absolute costs were then combined with estimates of standard metabolism to provide estimates of daily caloric cost during chase and non-chase conditions. The effect of chase on daily metabolism is then expressed as the *relative* (%) increase in daily caloric cost due to incorporating 1 chase of velocity x and duration y in 1 24 hour period.

Associated dolphins. Estimates for associated dolphins focus on estimating the cost to a mother dolphin of supplying the total energy costs (i.e., standard plus active metabolism) of a calf assumed to be subsisting entirely on milk from the mother, in addition to her own costs. Associated dolphins were assumed to be drafting or non-drafting mother-calf pairs. Drafting pairs were assumed to maintain the same velocity at all times so that total daily energy cost for the mother includes supporting an offspring swimming at either her V_{opt} or at some given chase speed. The V_{opt} for the mother rather than the calf was selected as the non-chase velocity for associated pairs because observations in the wild indicate that swimming velocity is primarily controlled by the mother regardless of the age of the calf (reviewed by Edwards 2001).

Energy costs to lactating females of supporting drafting offspring were calculated under two scenarios, both based on the assumption that an associated mother-calf pair would, under non-chase conditions, swim continuously at V_{opt} for the mother (i.e., about 170 cm/second for the 190 cm adult *Stenella*) and during chase conditions, the pair would swim at the given chase velocity for the given duration. The two different scenarios represent different assumptions about the nature of the mother-calf association called "drafting" (i.e., echelon swimming as described by Norris and Prescott 1961) in which a small animal (i.e., the calf) accompanies a larger animal (i.e., the mother) by traveling closely adjacent near the larger animal's midline, but without the smaller animal making any apparent movements of its fins or flippers.

Both scenarios assume that the total cost for the drafting mother-calf pair is simply the sum of the mother's cost at velocity x plus the cost of the calf moving next to the mother at the same velocity. Because the drafting animal is observed to make no movements (Norris and Prescott 1961, see also Edwards 2001), the first model scenario assumes that hydrodynamic drag on the calf is gliding drag only, which in the current model is 1/3 the drag on an actively swimming animal (i.e., the drag augmentation factor accounting for body and fin movements is eliminated from the equation for hydrodynamic drag). This (gliding) scenario should provide a reasonable approximation of the likely minimum cost to the mother of supporting a drafting calf because in this situation, the calf's active metabolism is significantly reduced compared to estimated non-associated costs. The second scenario assumes that the drafting calf incurs the same hydrodynamic drag as a non-drafting calf, so that cost to the mother is the sum of the individual drags estimated for the mother and for the calf, but where both mother and calf are swimming at V_{opt} for the mother (i.e., the calf is swimming faster than its own length-specific V_{opt}). This second (full-drag) scenario should provide a reasonable approximation of the likely maximum cost to the mother of supporting a drafting calf because the calf's active metabolism will be higher due to accommodating the mother's V_{opt} rather than the calf's.

These two scenarios were chosen in order to bracket likely costs because almost nothing is actually known about the physics of the drafting situation⁶. These scenarios should also provide reasonable brackets to the most likely situation in the ETP, in which mother-calf pairs maintain a close spatial relationship but in which actual drafting, at least after the first few weeks, is rare (reviewed by Edwards 2001). In this most likely situation, the calf is more likely to spend increasing portions of the day swimming at V_{opt} for the calf (reviewed by Edwards 2001), at least during non-chase times, which would produce costs to the mother intermediate to the costs estimated in the two scenarios described above.

Daily caloric costs were estimated for the mother and for the calf for each combination of chase velocity and duration, under both gliding and full-drag conditions. The sum of these costs was then taken as the total daily cost to the mother of supporting both her own and her calf's energy needs, under the assumption that the calf's total energy input was derived from the mother via milk. While it is unlikely that total energy input is still provided by the mother in calves over about a year of age (reviewed by Edwards 2001), this assumption was maintained even for the two-year old calf

⁶Only one study has considered the physics of drafting (Kelly 1956) and that study concerns the possible Bernoulli effects that might accrue to two adjacent spheres in a steady flow, rather than any specific investigation into drafting by smaller dolphins on larger individuals. The study concludes that "the idea of a porpoise getting a free ride is not at all unreasonable from the standpoint of hydrodynamic theory", but no useful quantitative results are presented.

for consistency and completeness. Also, it is a simple matter to generate approximate estimates of the reduction in cost to the mother if some or all nursing is replaced by independent feeding by the calf. The cost estimate for the for the mother can simply be decreased by the assumed fractional decrease in lactation vs. self-feeding. These estimates of total cost do not include inefficiencies in the cost of milk production and transfer because these costs, like specific dynamic action and urinary and fecal losses, are likely relatively constant over all conditions and also will be relatively small compared to the sum of active and standard metabolism.

Estimates are presented for total daily caloric cost for drafting (gliding and full drag) calves alone, mothers alone, and for the sum of mothers plus calves, as a function of calf size and chase velocity. Estimates are not presented as a function of chase duration because although *absolute* costs obviously increase with chase duration, the *fractional* increase in mother's cost due to associating with a calf was relatively constant (within 2-3 %) over all chase durations, due to the similarity in relative increases in costs to *both* mother and calf during increases in chase duration.

Estimates are also presented of the mass-specific power output required of mothers with drafting calves during chase under both gliding calf and full-drag calf scenarios, calculated on the basis of total body weight and also on the basis of propulsive muscle weight of the 190 cm TL mother. Mass-specific power output for mothers in mother-calf drafting pairs was estimated by summing the mechanical power estimates for both mother and calf at a given velocity and calf size, estimating total power requirement (PWR) by accounting for muscle and propellor efficiencies, and then dividing by either total body weight of the mother (70 kg) or by estimated weight of propulsive muscle (assumed 30% of total body weight, Figure 5).

RESULTS

Modeling results are compared in this section to existing reports of similar energy measures in other dolphins, both estimated and measured directly, in order to provide a general assessment of whether the model used here generates reasonably realistic results, as least for the range of energy costs for which comparisons with literature values can be made. Estimated energy costs are presented in a variety of formats (e.g., dynes, COT, watts, joules, calories; Figures 7-22) in order to facilitate comparisons with the variety of formats used in literature reports. Model estimates for adult *Stenella* are the only estimates for which comparisons can be made with other studies because power estimates do not exist for juvenile dolphins outside of the present model. However, consistent results for adults would provide encouraging evidence for model results for the smaller animals, as the power estimates for cost of swimming rely completely on physical variables and also are not affected by age differences in standard metabolic rate. Estimates of energy costs are presented in two sections, first for un-associated dolphins and second for associated (drafting) mother-calf pairs. Discussion of the implications of the results with respect to the influence of chase by tuna vessels on the energy costs of *Stenella attenuata* in the ETP are deferred until the Discussion section.

Un-associated dolphins:

Non-chase conditions (STD vs. ACT at Vopt). Because standard metabolism is not affected by active metabolism (ACT, i.e., doesn't change regardless of increases or decreases in time or velocity of swimming activity), model estimates of standard versus active metabolism are discussed here only

in regards to non-chase conditions, when active metabolism was assumed to consist of steady swimming at size-specific V_{opt} for each size of dolphin for all 24 hours of each day. Using Heusner's (1982) formulation for the relationship between standard metabolism generated reasonably realistic estimates of absolute rates of STD and also of the relationship between standard and active metabolism as a function of size. Estimated energy costs of standard plus active (swimming at V_{opt} for 24 hours) metabolism ranged from about 1×10^6 - 7.5×10^6 calories per day for neonate through adult dolphins, with swimming cost approximately twice the cost for standard metabolism in the adult dolphin compared to nearly equal expenditures on standard and active metabolism in neonates (Figure 6).

These appear to be reasonable estimates and patterns compared to existing reports. With respect to the estimated increase in standard relative to active metabolism in younger *Stenella*, studies on seals have shown that weight specific standard metabolic rate of young animals is often as much as twice that of adults (Ashwell-Erickson and Elsner 1981, Lavigne et al. 1982). Similar increases in weight-specific metabolic rate in younger animals are also commonly observed in other mammals (e.g., Brody 1945, Blaxter 1989). In terms of absolute calories expended daily in standard metabolism, the estimate here of approximately 2.3×10^6 calories per day for the adult *Stenella* (70 kg) compares well with the measured rate of 2.4×10^6 calories per day for a 68kg *Stenella attenuata* (Edwards 1992, using data from Hampton and Whittow 1976). This rate corresponds to 0.45 mg O₂/gww/hour (assuming 3.25 cal/mg; Elliot and Davidson 1975) and is consistent with resting metabolic rates of 0.3-0.6 mg O₂/gww/hr reported for bottlenose dolphins under various conditions (Hampton et al. 1971, Karandeeva et al. 1973, Hampton and Whittow 1976).

In terms of the relationship between standard and active metabolism in adults, the model estimates that active metabolism during constant swimming at V_{opt} (which can be assumed to simulate reasonably natural conditions) produces an estimate of active metabolism that is approximately twice that of standard metabolism. This corresponds well to the common observation that active metabolism of animals in nature is often about twice that of standard metabolism (e.g., Hui 1987 and references therein pages 130-131, Blaxter 1989, Table 9.6, using data from Nagy 1987).

In term of estimated total calories expended per day as a fraction of body weight, the model predicts that under non-chase conditions an adult *Stenella attenuata* would require approximated 7.5×10^5 calories to support the sum of standard and active metabolism. Assuming that the caloric density of this 69.73 kg animal is 1867 calories/gww (Edwards 1992) then the total animal contains approximately 1.3×10^8 calories. Assuming that *Stenella* prey is approximately the same caloric density as *Stenella* itself (i.e., primarily protein with some fat), then dividing 1.3×10^8 by 7.5×10^5 yields an estimate of daily energy input of approximately 5.8% body weight per day. This compares well with reported daily feeding rate of 5% body weight per day in 2 non-lactating adult female *Tursiops truncatus* approximately 145kg, 230 cm TL in captivity (Cheal and Gales 1991). At one year after parturition, while still actively lactating, both animals had increased their daily food intake to about 8% body weight per day, which compares well with a total cost of 7.8% estimated by the model for a mother feeding a 1 year old calf entirely dependent on milk (i.e., 2.7×10^6 calories per day required by calf plus 7.5×10^6 calories per day required by mother, divided by 1.3×10^8 total calories in mother's body).

Chase conditions:

Velocity effects on ACT (whole animal effects). Patterns in energy cost estimates under chase conditions of course directly reflect the formulations used to estimate the costs. For example, estimated whole animal hydrodynamic drag (in dynes, Figure 7) and weight-specific cost of transport (COT, in $\text{Joules kg}^{-1} \text{m}^{-1}$, Figure 10) both increase as the square of velocity, although drag *increases* with body size while weight-specific COT *decreases* with body size. Power estimates (velocity-specific measures; in watts) of whole animal mechanical power required to overcome drag (Figure 8) and total muscle power required to swim (Figure 9) increase even faster with velocity due to the cubic relationship between velocity and power requirements. *Weight-specific* power estimates (watts/kg; Figures 11-14) show the cubic relationship with velocity but the inverse relationship with body weight, as seen previously in the relationship between (weight-specific) COT and velocity.

Model estimates for drag (in dynes or newtons) experienced by 190 cm adult *Stenella attenuata* in the ETP compare well with drag estimates derived from video films of 3 non-instrumented free-swimming *Tursiops truncatus* approximately 200 cm in length and 245 kg in wet weight (Skrovan et al. 1999). Drag estimates from videos of the *Tursiops* for velocities of 1, 2, and 3 m/second were approximately 4, 16, and 38 Newtons respectively. Model estimates for adult *Stenella attenuata* swimming the same speeds were approximately 3, 10, and 20 Newtons (data derived from results for dynes, Figure 7). The lower estimates for the 190 cm *Stenella attenuata* are to be expected given the 3-fold difference in body weight (and thus likely 2-fold difference in wetted surface area) between the *Tursiops* and the *Stenella*.

There are no comparative studies to evaluate model estimates of mechanical power required to swim (in watts, Figure 8) but the results are illustrated here for completeness. A few comparisons are possible with the estimate of total muscle-produced power required to overcome drag (Figure 9), but more comparisons are possible when data are presented on a weight-specific basis, as will be discussed below.

Velocity effects on ACT (mass-specific). Comparisons do exist for estimated cost of transport (COT). Cost of transport can be expressed either as $\text{J kg}^{-1} \text{m}^{-1}$, or after dividing that expression by 9.8, as $\text{J N}^{-1} \text{m}^{-1}$ (see Yadzi et al. 1999 for details). COT is expressed here in the former units as these are more commonly reported. Most existing estimates of COT pertain to estimates of minimum cost of transport, which in the model presented here presumably occurs at V_{opt} for each size of dolphin. Model estimates of COT at V_{opt} range from about $2.5 \text{ J kg}^{-1} \text{m}^{-1}$ in neonates swimming about 120 cm/second to about $2 \text{ J kg}^{-1} \text{m}^{-1}$ in 190 cm adult *Stenella attenuata* swimming about 170 cm/second in the ETP (Figure 10). There are no existing comparisons with neonate or juvenile dolphins, but the model estimate of COT for adult *Stenella* compares well with measured and estimated COTs of approximately $1.2\text{-}2.9 \text{ J kg}^{-1} \text{m}^{-1}$ for a variety of dolphins under a variety of conditions, swimming 2-3 m/second (Worthy 1987, Williams 1993, Williams 1998, Yadzi et al. 1999). Model results also correlate reasonably well with a minimum total COT of $2.3 \text{ J kg}^{-1} \text{m}^{-1}$ calculated for a 70kg *Stenella* using Williams' (1999) allometric expression for swimming marine mammals swimming.

Comparisons also exist for estimated mass-specific power output where total body weight is used as the mass-specific measure, primarily for speeds approximating V_{opt} for *Stenella attenuata* (Figures 11 and 12). Comparisons do not exist for mass-specific power outputs based on weight of *propulsive* musculature but estimates are presented here for *Stenella* (Figures 13 and 14) in the interest of determining possible limits to *Stenella* performance (see Discussion section).

In some cases, model results are presented for both the full range of velocities simulated and for a reduced range up to 3 m/second. Both figures are presented because energy costs increase so rapidly with velocity that the estimates at the lower speeds, for which most comparisons exist, are obscured in the figures that include the full range of estimated velocities.

Model estimates compare reasonably well with published reports of mass-specific power output, both at common routine speed and at higher speeds. Model estimates of total body mass-specific power output at V_{opt} s ranging from about 120 cm/second in neonate to about 170 cm/second in adults are approximately 3 watts/kg for all sizes of dolphin (Figures 11 and 12). This compares reasonably well with measured mass-specific power outputs, derived under various methods, of about 2.5-5.5 watts/kg for various adults of species of dolphins either resting or swimming at about 2 m/second (Hui 1987, Worthy 1987, Williams 1992, Fish 1993, Yadzi et al. 1999).

Relatively few measurements (as opposed to purely model estimates) exist of energy costs during swimming faster than routine speeds. Although a number of studies present a variety of estimates of drag, thrust power, and metabolic power at various swimming speeds for a variety of dolphins (reviewed by Fish and Rohr 1999) most of these estimates are based either on completely different models (and therefore not comparable) or are based on models using generally the same formulas as used here, but with varying assumptions about model parameters such as propulsive efficiency, metabolic efficiency, drag formulation, body morphology (e.g., wetted surface area, surface area of fins, wet weight, maximum diameter) and so forth. Comparisons with those modeling results are not appropriate unless the parameter estimates and formulae are the same as used here, which they aren't.

Of the studies presenting results of direct measurements on swimming dolphins, only 2 provide direct measurements of total metabolic costs during swimming at various speeds (Williams et al. 1993 and Yadzi et al. 1999). The other studies determine drag and power output from analysis of still pictures, movies, or more recently, videos, of gliding or in 1 case (Fish 1993) actively swimming dolphins. Of these picture-based analyses, the most appropriate for comparison are the two most recent (Fish 1993 and Skrovan et al. 1999) because these studies use the most current methods in model formulation, the most current information about model parameters values, and the fewest estimated parameters. Therefore these 4 studies will be used to compare with the model results presented here.

Model estimates of thrust power output for the 190 cm *Stenella* compare well with thrust power estimated as a function of velocity from videos of 5 *Tursiops* swimming between 1 and 6 m/second (Fish 1993). Converted to W/kg total body assuming an average *Tursiops* weight of 230 kg, estimated weight-specific thrust power for velocities of 1, 3, 5, and 6 m/second is 1, 3, 14, and 23 W/kg for these *Tursiops*, compared to model estimates here for *Stenella* of 1, 3, 13, and 21 W/kg respectively. These comparisons refer to mechanical power output only, because Fish's analysis does not include metabolic efficiency. Assuming the same metabolic efficiency for the *Tursiops* in Fish's study as used in the present model (i.e., 0.2), an estimate of total power output by his *Tursiops* swimming at 6 m/second is 115 W/kg ($=23*(1/0.2)$), which compares reasonably well with the model estimate of about 125 W/kg (Figure 25). Fish reports a maximum estimated thrust power for *Tursiops* in his study as 7600 watts at 5.9 m/second. Assuming the animal weighed about 245 kg, estimated mechanical power output is about 31 W/kg, with estimated total power output of 155 W/kg ($=31*(1/0.2)$). This also compares reasonably well with the estimate of 125W/kg for a 190

cm *Stenella* swimming 6 m/second.

Model estimates of metabolic rate for 190 cm *Stenella* (approximately 70 kg) also compare reasonably well with observed metabolic rate of 2 Tursiops (avg 162 kg) swimming for brief periods in a small (15m diameter) pool (Yadzi et al. 1999). Observed average metabolic rate at 2 and 3 m/second were approximately 2.5 and 3.7 W/kg compared to approximately 2.9 and 5.9 W/kg estimated for *Stenella* swimming the same speeds. The observed values were calculated from oxygen consumption so represent metabolic rather than merely mechanical power. The somewhat lower observed values for *Tursiops* may be related to the greater than two-fold difference in body weight between the species, but may also result from the fact that the metabolic rate measure represents costs accrued over some interval, during which the *average* speed was reported, but during which both faster, and more likely, slower speeds were occurring, which would generate a lower estimate overall.

Comparisons of model estimates cannot be made with *directly measured* energy costs for *sustained* swimming faster than about 6 m/second because no such data exist. Voluntary swimming speeds, even for trained and presumably motivated dolphins, rarely seem to exceed about 6 m/second, with speeds of about 2 m/sec much the norm (e.g., Hui 1987, Williams 1992, Williams 1993, Skrovan 1999, Yadzi et al 1999, Fish and Rohr 1999). Comparisons can be made with other *estimates*, particularly of power expressed as W/kg total body, because power output by swimming dolphins has been of interest since Gray (1936). In general, those estimates tend to be for maximum or burst power output, rather than for sustained speed, partly because dolphins in general decline to swim much faster than 2-3 m/second for any period of time⁷. Unfortunately, these existing estimates tend to be quite variable due to the variety of methods, models, and assumptions that have been used to derive them (Fish and Rohr 1999), therefore comparisons with model estimates produced here would in most cases be inappropriate.

For example, the model presented here estimates that about 212 watts are required for a 190 cm *Stenella attenuata* to overcome drag while swimming at 3 m/second (this is mechanical power required, not total body power which will be much higher due to muscle and propellor inefficiencies). This compares poorly with an apparently similar estimate presented by Hui (1987) of 68 watts for adult *Stenella* swimming the same speed, using an equation that appears quite similar to that used in the present model. The difference in power estimates results primarily from very different assumptions about the augmentation of drag required to account for movements of body, fins and flukes. Hui used an augmentation factor of 0.2 based on the best information available at the time, when no direct measurements of energy cost of swimming had yet been conducted on living dolphins. Since then, estimates derived from observations on living animals has shown that the factor should be about 3, i.e., 15 times greater (e.g., Skrovan et al. 1999 and

⁷For example, apparent swimming speeds of tagged *Stenella attenuata* before, during and after chase and capture by tuna vessels ranged from about 1.5-3 m/second under all conditions (CHESS cruise 2001, Chivers data).

references therein), at least within the speed ranges measured to date.

Duration effects. Cost of chase in terms of work performed during chases of varying duration (i.e., power*time) is presented here in terms of whole animals only. Results are presented in absolute terms in only one case (1 60-minute chase, Figures 15 and 16) in this section, as an example of model results, but the majority of the estimates of cost of chases of varying velocities and durations are presented in relative terms as estimated percentage increase over daily (24-hour) non-chase caloric cost, due to incorporating 1 chase of a given velocity and duration within 1 24-hour period. This formulation of relative costs was chosen because it facilitates understanding of the cost of chase compared to normal conditions.

Work estimates for 1 60-minute chase (Figures 15 and 16) also show the expected rapid increase with velocity, as do the estimates of percent increase in daily cost due to 1 chase of 15, 30 or 60 minutes duration (figures 17-22). The work estimates for absolute costs in Joules or calories are shown only for one chase duration because deriving estimates for other durations is a simple matter of dividing by 4 (for a 15-minute chase) or 2 (for a 30-minute chase). Work estimates in relative terms (i.e., estimates of percent increase) are presented in full and reduced scale for all three chase durations to facilitate discussion of the implications for *Stenella attenuata* in the ETP.

Figures 17-22 all show negative estimated percentages at the slowest chase speeds for all sizes of dolphins, with the negative percentages occurring at progressively slower speeds in the smaller dolphins. This occurs because the percentages are calculated in relation to the estimated V_{opt} for each dolphin size, and this V_{opt} exceeds the slower chase speeds for all sizes of dolphins. The percent difference in daily caloric cost does not become positive until the chase speed exceeds the V_{opt} for a particular size of dolphin. In reality, chase speeds below a couple of meters per second are not especially likely but results for the slower speeds were included here for completeness.

The direct relationship between energy costs and duration of chase are very clear in Figures 17-22, which show a doubling of energy cost increases when chase duration is doubled from 15 to 30 minutes, with doubling again from 30 to 60 minutes. For example, estimated percent increase in calories expended by an adult (190 cm TL) *Stenella* swimming about 3 m/second is about 3% for a 15 minute chase, 6% for a 30 minute chase, and 12% for a 60 minute chase.

Figures 17-22 also illustrate that higher chase speeds and longer durations become costly very quickly for ETP dolphins, with costs rising most rapidly for the smaller dolphins due to their smaller energy production capacity (i.e., less muscle available to provide swimming power). For example, estimated increase in daily cost due to 1 30-minute chase at the maximum estimated speed of 7.5 m/second ranges from about 90% for a 190 cm TL adult *Stenella* to about 160% for a neonate (Figure 18). Even for chases at velocities on the order of 5 m/second, estimated cost increases due to 1 30-minute chase range from about 30% in adults to about 50% in neonates. Estimates of energy cost increases for the slower chase speeds are more ecologically realistic. Estimated increases due to 1 30-minute chase at 3 m/second range from about 6% in adult *Stenella* to about 12% in neonates (Figure 21).

Direct comparisons of these estimated energy costs and increases in energy costs due to chase cannot be made with existing reports because none exist for increases in feeding rate with increasing swimming speed in dolphins. However, general comparisons, and more importantly, likely limits can be derived from observations of feeding rates for other large wild mammals. As

mentioned previously, the model estimates of daily food intake in adults under non-chase condition of about 5% per day is very similar to observed feeding rates in similar dolphins. This feeding rate is also reasonable for a basically carnivorous mammal the size of dolphins. Given that the estimated non-chase feeding rate is realistic, and that estimated energy expenditures for speeds up to about 6 m/second correlate well with observed expenditures in living dolphins, it seems reasonable to accept the estimated energy increases due to chase as at least approximately realistic. Discussion of the implications of these results for *Stenella attenuata* in the ETP are deferred until the Discussion Section.

Associated dolphins:

Whole animal estimates. Model estimates indicate that motherhood is energetically expensive (Figure 26). Supporting the energy needs of a calf is apparently quite costly even for a newborn calf and increases with size (age). For the model formulae used here, the added daily cost of supplying energy needs for a continually associated calf of a given size and drafting condition (i.e., gliding or full drag) is essentially a constant added fraction of the mother's daily cost for all chase durations and velocities due to similar *relative* increases in both calf and adult costs with increasing duration and velocity. Thus, the added cost of a calf can be summarized as a single fractional increase for each size of calf under all chase conditions (Figure 23). Given the assumptions used here (i.e., that cost of drafting calves is due only to gliding drag plus standard metabolism, that continually associated calves move at V_{opt} for the mother, and that gliding drag is 1/3 the cost of drag on actively swimming dolphins), it appears that supporting a continually glide-drafting calf is much less costly than supporting a continually drafting, full-drag calf, i.e., one third the cost. An generally associated but non-drafting calf would be intermediate in cost. Thus, estimated increase in mother's daily caloric cost for drafting calves ranges from about 7% per day for neonates to about 16% for a 1-year old calf, and from about 21% to 48% for non-drafting calves of the same age. Thus whatever the total daily caloric cost estimated for an unassociated mother dolphin for any chase velocity and duration, her cost with a continually associated calf will increase that unassociated cost by the appropriate percentage for a calf of a given size and drafting condition.

The estimate of percent increase in energy cost for mothers of 1 year old calves (129 cm TL), ranging from 16% for gliding calves to 48% for full-drag calves, compares reasonably well with the observed average increase of 52% for 3 lactating mother *Tursiops* with calves at 1 year after parturition (Cheal and Gales 1991). The higher estimate (for full-drag calves) is more realistic because by 1 year of age dolphins calves are well past the age of drafting (reviewed by Edwards 2001).

Although the percentage increases remain basically constant regardless of chase velocity or duration, the *absolute* costs of the mother-calf system increase markedly with both velocity and duration, as observed previously for un-associated dolphins. The absolute costs for drafting calves of each size gliding or full drag, the cost for the mother without a calf, and the cost for a drafting or non-drafting mother-calf association, appear in Figures 24-27, in order to summarize the relationships in picture form for easier comprehension. The cost of a small calf is a relatively small fraction of the mother's individual cost, but that fraction increases steadily with increasing calf size. Figures are presented only for the 30-minute chase. Results for 15 and 60 minute chase can be estimated easily as 1/2 or 2 times the predicted cost for a 30-minute chase.

Mass-specific measures. Estimated mass-specific power output required of the mother reflects the rapid increase in power required to carry a calf at increasing velocity and with increasing calf size (Figures 28-35), but the relative increases are the same as originally presented in Figure 26. For example, carrying a gliding neonate increases the mother's weight-specific cost by about 7%, while carrying a full-drag drafting neonate would increase that cost by about 22%. Discussion of the implications of these cost estimates for *Stenella* responses to chase in the ETP are deferred to the next (Discussion) section. There are no comparable data in the existing literature.

Model veracity.

These similarities between model estimates of a variety of energy measures and a variety of laboratory and field measurements on live animals provide encouraging evidence that the model is generating reasonably realistic estimates of energy costs for *Stenella attenuata* in the ETP, at least under normal (non-chase) conditions. Although direct comparisons are not possible for the higher speeds, the model presented here incorporates the most current data specifically available for *Stenella attenuata* in the ETP and the most appropriate formulations available to utilize these data, based on current understanding of dolphin swimming hydrodynamics and energy costs.

The results presented here are simply the numerical estimates generated by the model formulation described above, given the parameters supplied to the model. The ability to calculate an estimate does not imply that the results are ecologically meaningful or possible, but the results, if model results can be accepted to reasonably accurately reflect actual costs to living dolphins in the real world, can be useful for determining likely ecological or physiological limits to *Stenella* activities during chase by tuna vessels in the ETP. In general, recent studies as well as model results presented here indicate that dolphins do not appear to be capable of anything particularly unusual for mammals in terms of energy production (e.g., Fish and Hui 1991, Williams 1999). The following (Discussion) section uses the results presented here to suggest likely limits on *Stenella* performance *in situ* and discussed these limits with respect to potential energy-related effects of chase by tuna vessels on *Stenella* in the ETP.

DISCUSSION

Adult Energetics.

Unassociated adults. The effect of 1 daily chase can have a small to large effect on energy output for the day of chase, depending on the length of chase (Figures 17-22). At the most likely chase speeds of about 3 m/second (discussed below), estimated increased energy costs for that day range from about 5% in adult *Stenella* to about 12% in neonates. Estimated energy cost increases are half that for a 15 minute chase and double for a 1 hour chase. While the estimated cost increases for a full-hour chase are quite high, the long-term energetic consequences for un-associated *Stenella* of even chases of this duration are probably relatively small overall. This is because repaying the energy loss during chase can be integrated over the relatively long *inter-chase* periods likely to pertain in the ETP. It appears that dolphins in the ETP may be set on, on average, about 8 times per year, with dolphins in smaller aggregations less likely to be chased while dolphins in large schools may be chased much more frequently (Edwards and Perkins 1999).

Mother-calf (drafting) pairs. During drafting, the massive size of the mother compared to the sizes of calf that are likely to be drafting (i.e., up to about 98 cm or 3 months of age at most, reviewed by Edwards 2001) leads to estimated increases in cost to the mother that are relatively minor and reflect

the overall increases presented earlier - i.e., an increase in energy costs of 7% for a drafting gliding neonate (85 cm TL) to about 10% for a 3-month old 98 cm calf or for drafting full-drag calves, an increase of 22% for a neonate to 29% for a 3-month old calf (Figure 23).

These estimates of power output for the mother in cow-calf pairs show clearly the energetic advantage to having a calf associate via gliding drafting (Figures 28-35). This mode of movement is significantly less expensive (i.e., about 1 third the cost of a full-drag calf) both in terms of short-term power output and in terms of daily overall cost of providing the energy needs of the calf. These obvious energetic advantages to the mother lead to the question of why drafting decreases rapidly with age (reviewed by Edwards 2001) if it seems so advantageous to the mother. The answer likely relates to the need for the calf to become independent in order to provide for its own muscular and behavioral development, and also the need for the mother to successfully forage in order to support herself and her offspring. It is difficult to imagine successful foraging while attached to a drafting calf, and in fact it has not been observed except in captive situations where mothers with drafting calves will sometimes accept food thrown to them as they swim by in formation (reviewed by Edwards 2001). These are probably the main reasons that the drafting relationship tends to disappear within the first few weeks or months of life for dolphins. Once that direct physical relationship ends the calves are then responsible for keeping up with their mothers, and through their mothers with the school, on their own.

Because gliding drafting is the most likely scenario in the ETP and because it likely persists at any high level only until the calves are about a month or two old (i.e. 90-98 cm TL) the *additional* power output required of the mother in the drafting pair will be relatively small compared to the energy she is already expending for herself (Figures 28-35). This added cost would likely affect her ability to maintain speed with the school only during chases of longer duration as her overall power supplies become progressively depleted compared to unencumbered animals. If drafting could be maintained during chase (not likely, discussed below), chases of less than about half an hour likely might not cause glide-drafting mother-calf pairs to fall significantly far behind the faster unencumbered adults. Thus, the cost of chase does not seem extremely critical to the mother in a mother-calf pair, at least for relatively short and infrequent chases.

Thus, the energetics consequences of chase do not appear to be very significant for adult *Stenella* in the ETP, including mothers in mother-calf pairs. The same cannot be said for their calves.

Calf Energetics.

Size-related energetic limitations during chase.

The question of whether chases by tuna vessels may be having adverse effects, and in particular, size-related adverse effects on *Stenella attenuata* in the ETP can be examined by determining the relationships between swimming speeds, the sustainable (energy-based) duration of those speeds, and the power that is required to maintain those speeds, for chase situations in the ETP. Comparisons with existing reports indicate that model estimates of power outputs for *adult* *Stenella* are reasonably realistic, at least for velocities up to about 6 m/second. Examination of existing literature also provides reasonable estimates for the length of time (i.e., duration) that adult *Stenella* can likely maintain various speeds (Table 2). Based on data from Table 2, it appears that *adult Stenella* can likely swim at 6 m/second for a 1-2 second burst, at 5 m/sec for a few seconds to perhaps a minute, at 3 m/second for several to many minutes, at 2 m/sec for hours and at 1.5 m/sec

indefinitely. The determinations are for adult *Stenella* because the data in Table 2 are derived from adult animals.

Velocity limits. Given this reasonable range of likely speeds, durations, and power outputs for *adult Stenella* it is possible to estimate potential limits to speeds and durations achievable by the younger (smaller) animals. This can be done by assuming that the mass-specific power output of adults required to maintain a particular *duration* of swimming at some speed is the species-specific maximum amount of time at which any size (age) of *Stenella* can maintain a power output of that level. This approach is based on the observation that the ability to swim a particular speed for a particular time (for any animal) decreases with increasing time. For example (from Table 2), a *Tursiops* was able to swim 8.3 m/second for 7.5 seconds, 6 m/second for 50 seconds, and about 3 m/second indefinitely. By relating power output to the *duration* of time it can be maintained, it is possible to estimate the *speed* that could be maintained for that duration, by the smaller animals.

For example, the model estimates that mass-specific power output for adult *Stenella* swimming 6 m/second is about 400 W/kg propulsive muscle⁸ (Figure 13). Literature reports indicate a duration of a second or two for swimming speeds of about 6 m/second. By assuming that 400 W/kg propulsive muscle is the maximum power output that can be maintained by *Stenella* musculature for a second or two, for *any size* of *Stenella*, then the model results can be used to determine the speeds at which smaller *Stenella* expend 400W/kg propulsive muscle. Examination of Figure 13 indicates, for example, that neonate *Stenella* generate about 400 W/kg propulsive muscle while swimming about 3.2 m/second. Thus, it appears that the maximum burst speed of which neonate *Stenella* are capable is about 3 m/second, compared to 6 m/second for the adult.

Similar calculations can be made for each assumed power output per duration (Figure 36). The model indicates that *Stenella* calves cannot swim as fast for as long as adults and that for the younger calves the difference in estimated abilities is quite large. This result has serious implications for the ability of smaller dolphins to maintain the speed of adults during a chase by tuna vessel speedboats (discussed below).

Power output limits. A related calculation pertaining to size-specific differences in energy production capacity in *Stenella attenuata* in the ETP compares the mass-specific power output that is required by adults to swim at various velocities, with the power outputs for smaller *Stenella* to swim the same speed. It turns out that the relative difference is the same across all velocities for a particular size. For example, model estimates indicate that a neonate *Stenella* must produce 4.6 times more watts per kg of propulsive muscle than an adult swimming the same speed (Figures 13

⁸Because muscle proportion of body weight decreases with size in *Stenella attenuata* in the ETP (Figure 5), the most appropriate measure of power output is W/kg propulsive musculature rather than simply W/kg total body weight.

and 14). The factors are 4.4, 4.2, 3.5, 2.8, 2.1, and 1.5 times adult power outputs for 87, 90, 98, 110, 129, and 154 cm *Stenella* ranging from 1 week to 2 years of age. These higher power outputs for a given velocity mean that the calves will be able to swim those velocities for a much shorter time. Again, these estimates generate serious doubts about the ability of *Stenella* calves, particularly the younger ones, to maintain adult speeds during chase by speedboats, i.e., to keep up with the school.

While these estimated limits to calf performance are impressive and troubling, they are probably significant *underestimates*, at least for calves less than about 6 months old. The estimates above are based on the assumption that a kg of propulsive muscle from a calf will be as efficient in producing power as a kg of propulsive muscle from an adult. This is very likely not the case.

Other studies related to limitations on calf power production capacity

Three recent studies on a variety of other dolphins, including the closely related spinner dolphin (*Stenella longirostris*; Dolar et al. 1999) have shown that dolphin calves are born with significantly diminished aerobic capacity (i.e., power production capacity) compared to adults, and that it takes months to years for various aspects of that aerobic capacity to reach adult levels.

In the first study, Dolar et al. (1999) observed muscle color and measured myoglobin (Mb) concentration in swimming muscle (longissimus) from 4 spinner dolphin calves ranging in size from 115-123 cm TL and from 4 Frazer's dolphin calves (98-150 cm TL), as well as in a number of adults of both species. All animals were from wild populations and were killed incidentally in drift net fisheries. They found that muscle color in calves was light pink⁹ compared to dark or almost black in adults, reflecting the measured increases in Mb content from about 2 g per 100g muscle in neonates to about 5.5 g per 100 g muscle in adults, i.e., young calves had only about 1/3 the Mb content of adults. These differences in Mb concentration contributed to a nearly threefold difference in estimated muscle oxygen capacity from calves through adults, from 30 ml O₂ kg⁻¹ muscle in calves to 84 ml O₂ kg⁻¹ muscle in adults, i.e., the younger dolphins had only about 1.3 the muscle oxygen capacity of adults. These data are particularly troubling with regards to the situation for neonate *Stenella* in the ETP, because the animals in Dolar et al.'s (1999) study were at least several months old. Differences are likely greater for the younger dolphins, particularly neonates, based on the results from two additional studies.

⁹Light pink musculature was also observed for all the smallest *Stenella* calves (actually very late-term fetuses) compared to very dark red in the adults sampled from the ETP tuna purse-seine fishery (Edwards, unpubl. Data)

The second study (Dearoff et al. 2000) examined muscle fiber types and muscle histochemistry in bottlenose dolphins (*Tursiops truncatus*) in order to compare bottlenose calves with other locomotor-precocious young in terrestrial mammals (e.g., wildebeest calves). In this study, samples were collected from adult and neonate stranded *Tursiops*, where all *Tursiops* calves were assumed to be less than two weeks of age, based on the continued floppy condition of the flukes¹⁰. Muscle fiber type composition (i.e., fraction of slow twitch vs. fast twitch muscle) was found to be similar between calves and adults, but neonate muscle fibers differed from adults in distribution of mitochondria and lipid content. These differences in distribution indicate that neonate *Tursiops* have lower aerobic capacity than adults, which in terrestrial animals (and presumably in dolphins) translates to decreased motor stamina. In terrestrial animals, this results in even precocial neonates not being able to locomote at high speeds for long periods of time (Estes 1991, Carrier 1994, 1995, quoted in Dearoff et al. 2000).

The third study (Noren et al. in press) measured various characteristics of blood oxygen storage capacity in captive and wild *Tursiops* ranging in age from neonates through about 12 years old (i.e. reproductive adults). Samples were collected from 6 calves between 0-1 month of age, 7 at 5-6 months, 4 at 11-12 months, and 6 at 17-18 months, and 4 at 23-24 months. Pronounced changes in several parameters associated with increased oxygen storage capacity occurred between birth and about 6 months of age, with continued but slower changes occurring over the next 2-3 years. Blood parameters did not reach adult levels (in both captive and wild *Tursiops*) until the calves were nearly 3 years old. Specifically, total mass-specific oxygen stores essentially doubled (from 18 to 30 ml kg⁻¹) during the first three years and then remained basically steady thereafter. In a related calculation, estimated aerobic dive limit (*not* accounting for increased metabolic rate in younger animals) was only 1.6 minutes at birth, increasing to 3.2, 3.6, and 4.8 at 1, 2, and 3 years of age.

All three of these studies show very significantly reduced power production capacity in neonate dolphins, with relatively slow approach to adult levels taking on the order of months to years before calves reach adult capacities. It appears that power production capacity (i.e., watts per kg propulsive muscle) in neonate *Stenella* may in fact be a few to several times lower than adult capacity, for at least the first few weeks or months, rather than similar as assumed in the model results discussed above. If so, then the likelihood of separation during chase may be significantly greater than the already high likelihood indicated by those model results. This bodes ill for calf survival because separation for any length of time (i.e., on the order of an hour or more) is likely to be lethal for *Stenella* calves separated from their mothers (and their school) in the ETP (discussed below).

Likelihood of separation of calves from mother (and school) during chase.

Drafting during chase: The power limitations discussed above for calves presumably could be overcome if the calves could maintain a drafting relationship with their mothers during chase, because then the calf would be relieved of the energetic burden of trying to keep up with the school.

¹⁰Observations on fin condition in neonate *Tursiops* indicate that flukes do not become stiff for about 2 weeks (McBride and Kritzler 1951). If the same is true for *Stenella* calves in the ETP (highly likely), then likelihood of loss of neonates during chase is even higher than discussed above.

The burden of association in the drafting would fall to the large adult. The drafting relationship would provide a means for an energy-limited calf to move at higher speeds for longer periods that would be possible without drafting. It is obviously a cost-effective way for the mother to support and protect her calf, at least for the first few weeks or months, and would relieve the calf of the burden of trying to keep up independently using its own seriously inadequate power plant.

Unfortunately for *Stenella* calves, it is not likely that the drafting relationship can be sustained for long under chase conditions. This is because as velocity increases, respiratory rate will increase, and therefore surfacing frequency will increase for the mother. While breathing tends to be synchronized for mother-calf pairs under normal conditions (reviewed by Edwards 2001) with likely speeds around 1.5 m/second, under chase conditions the animals will be moving much more quickly, using much more energy (due to the cubic increase in power output requirement with increasing velocity), and therefore will be both breathing more often and breaking the surface more rapidly. It is difficult to imagine how the drafting relationship could be maintained through any surfacing event, which would presumably completely disrupt the Bernoulli flow that likely supports the relationship. Once disrupted, the relative velocities of the two animals will change due to the enormous difference in mass between mother and calf. The faster the mother's speed, the greater will be the relative change. The calf will be left behind, and the mother will have to alter her speed to reestablish the relationship. However, because the mother's activity during chase will most likely be a fright-flight reaction, the mother is likely to be more motivated to stay with the school than to stay with her calf (reviewed by Edwards 2001). Thus, it is quite likely that the calf will at some point be left on its own to maintain speed with the school, where school speed is most likely to be set by the largest unencumbered and terrified adults. This will not be good for the calf, given the significantly reduced power output and swimming duration capacities estimated for smaller *Stenella*.

Swimming independently during chase. Given that drafting is not likely an option for even neonate *Stenella* calves due to physical disruption of the relationship during high-speed swimming, and that drafting by calves older than a month or two is not tolerated by mother dolphins anyway, it appears likely that performance capacities of un-associated calves will likely control the rate of calf separation during chase. The situation does not look very encouraging for any *Stenella* calves under a year or two of age. These calves are apparently still much too small and relatively weak to maintain adult speeds for very long. Their aerobic processing capacity is also likely still reduced. Thus, the faster and/or the longer the chase, the more likely it appears that calves will be left behind. While a chase of a few minutes may not pose a great problem, chases of even half an hour or more may lead to significant calf loss. The duration of the chase is likely more important than the speed, given the power/duration relationship. If a fast chase can be concluded quickly, it is more likely that calves could achieve the required power output during the short time it was needed. As chase duration increases however, power output capacity decreases rapidly, so that more and more calves are likely to be lost because they have exceeded their ability to keep up.

For example, if a *Stenella* (of any size) is able to produce 57 W/kg propulsive muscle for some number of minutes, then an adult *Stenella* can swim at about 3 m/sec for those minutes, but a neonate will only be able to swim about 1.5 m/sec for the same number of minutes, because a neonate can only swim 1.5 m/second while expending 57W/kg propulsive muscle. In order to swim 3 m/second, the neonate would have to expend about 264 W/kg propulsive muscle - but this level of

power output is likely sustainable only for a few seconds rather than for some minutes. So after a few seconds, the neonate's ability to keep up with the 3 m/second adult would be exhausted and the little animal would have to reduce its speed, thus falling progressively further behind.

Stenella calves might, in theory, be able to reduce their swimming costs during by employing a burst-and-glide mode (e.g., Au et al. 1988 and references therein). However, recent video studies of *adult Tursiops* swimming behaviors have shown that the burst and glide mode of swimming decreases with increasing speed (Skrovan et al. 1999), so that glide periods during steady-state horizontal swimming at 1.5-3.7 m/second rarely exceeded 2 seconds. The more difficult the swimming situation (i.e., the higher the drag), the less likely the dolphin will (can) use burst and glide strategies to reduce energy costs. At chase speeds it seems unlikely that burst and glide swimming will be possible for *Stenella* calves.

Based on the information presented above, it appears likely that the rate of calf loss will increase with both chase speed and duration, as the calf's capacity to keep up diminishes. For non-drafting calves up to at least a year old and probably older, it does not appear likely that calves and mothers can remain associated for long if the school as a whole swims at velocities chosen by frightened unencumbered adults, particularly given the apparent likelihood that frightened mothers will chose to remain with the school rather than slowing down to accommodate their calves (reviewed by Edwards 2001)

Consequences of separation. The significance of calf separation for subsequent calf mortality will likely depend mostly on the duration of separation. Studies of mother-calf behavior in wild *Tursiops* (reviewed by Edwards 2001) indicate that after the initial few days or weeks of uninterrupted drafting association between mother and calf, mothers increasingly begin to separate from their calves (and their calves from them). During mother-initiated separations, the general behavior of calves includes swimming in small circles in the area where the calf was left by the mother and constant whistling until the mother returns. If *Stenella* calves exhibit the same behaviors, it is difficult to imagine how they could survive separations of more than a few minutes without being located by the large predatory sharks that are common in the ETP, commonly observed outside (and sometimes inside) purse-seine nets during sets, and which presumably are rarely far from the excitement of a tuna/dolphin chase and set.

The possibility of calf loss to predation after separation from its mother could perhaps be mitigated if the separated calf was immediately re-united with another adult, but this is not likely. It would be physically impossible during chase for the reasons described above, and would be unlikely after chase because adoption is extremely rare in dolphins (reviewed by Edwards 2001). It might be possible for another adult to temporarily protect the calf until it could be reunited with its mother, but this would require the other adult to have been willing to separate from the school during chase in order to remain with the calf. It is difficult to imagine any adult being more motivated to do this than the mother herself, but even the mother is apparently not very likely to leave the school during chase.

Thus it appears that a calf separated from the school is likely to remain that way until its mother can relocate it. The amount of time this might take will depend on the relative positions of the calf and the mother at the end of chase. If the mother has escaped the net and can hear her calf, then reunion should take place on the order of minutes and the calf will be more likely to survive, depending on the predator concentration at the time. If the mother successfully relocates her calf

before predators do, then the calf will likely survive the event. If the mother has been captured then the baby will be left to its own devices for at least an hour and perhaps longer, while the net is closed, the backdown channel created, and the dolphins released over the net. It is much more likely that predation will affect calf survival during this longer time period, and it is very likely that predation by sharks is a significant risk. Shark predation on dolphin calves is both well documented and very wide-spread (Heithaus 2001 and references therein).

Management Implications. Based on these observations, it appears that calf separation is quite likely during chase, with separation likelihood increasing with decreasing calf size and increasing speed and duration of chase. Subsequent mortality is also quite likely for separations exceeding minutes to hours, due to likely risk of predation on separated calves. Mortality risk will increase in likelihood with decreasing calf size due to decreased ability to escape and/or protect itself from attack.

Implications for management are that potentially significant calf mortality can be minimized by 1) avoiding setting on schools that contain calves, particularly young calves, 2) minimizing the duration of chase, and 3) minimizing the length of time dolphins are retained in the net. The second of these minimization strategies is already a fundamental part of the tuna-purse-seine fishery because shorter chases are both less expensive and tend to be more successful. The third strategy is probably also in effect, related to minimizing cost and the potential for dolphin mortality in the net. Thus, the only potential improvement that might be made under current conditions (i.e., while setting on dolphin calves is permitted) would be to concentrate effort on identifying and avoiding dolphin schools with calves, presumably by scrutinizing the school from the vessel's helicopter prior to initiating a set. This may or may not be possible, depending on the ability of observers in helicopters to spot calves from the air.

CAVEATS AND CONCLUSIONS

One potentially significant caveat that readers may wish to keep in mind regarding the modeling results presented here is that the results are presented as absolute values rather than with any sort of associated statistics. It is more likely that individuals of various sizes in real populations of *Stenella attenuata* in the ETP encompass a range of values for morphological, physiological and behavioral characteristics within each size, so that a range of responses is much more likely than some single response for a given size. This lack of statistical analysis can be a problem where responses tend to be subtle and therefore difficult to discern. However, the model results presented here with respect to size-related effects of chase on *Stenella* energetics in the ETP are far from subtle. While it is possible that some particularly strong calves might be able to stay with the adults during chases of relatively short duration, it is difficult to imagine how energy production capacities so much smaller than that of adult dolphins could not have serious and significant effects on calf separation and survival during and after chase by tuna vessel speedboats in the ETP.

In summary, the likely effect of chase on adult dolphins, including lactating females, appears to be relatively insignificant at chase frequencies on the order of 1 or 2 per month and given observed chase speeds of about 3 m/second. In contrast, the likely effect on dolphin calves appears to be profound, due to the high likelihood of calf separation during chase and the likely high risk of predation for calves whose mothers were captured during that chase.

LITERATURE CITED

- Alexander, R. M. (1999). One price to run, swim or fly?. *Nature* **397**, 651-653.
- Alexander, R. (1983). *Animal Mechanics*. London: Blackwell Scientific Publ..
- Archer, F., Gerrodette, T., Dizon, A., Abella, K. and Southern, S. (2001). Unobserved kill of nursing dolphin calves in a tuna purse-seine fishery. *Mar. Mamm. Sc.* **17**, 540-554.
- Ashwell-Erickson, S. a. R. E. (1981). The energy cost of free existence for Bering Sea harbor and spotted seals. In *The eastern Bering Shelf: Oceanography and resources*, vol. 2 (eds. D. a. J. C. Hood), pp. 869-899. Seattle: Univ. Wash Press.
- Au, D. and Perryman, W. (1982). Movement and Speed of Dolphin Schools Responding to an Approaching Ship. *Fishery Bulletin* **80**, 371-379.
- Au, D. and Weihs, D. (1980). At high speeds dolphins save energy by leaping. *Nature* **284**, 548-550.
- Blaxter, K. (1989). *Energy Metabolism in Animals and Man*. New York, USA: Cambridge Univ. Press.
- Brody, S. (1945). *Bioenergetics and Growth*. New York, USA: Reinhold Publ. Co..
- Carrier, D. (1994). Ontogeny of jumping performance in the black-tailed jackrabbit (*Lepus californicus*). *Zoology* **98**, 309-313.
- Cheal, A. and Gates, N. (1991). Body Mass and Food Intake in Captive, Breeding Bottlenose Dolphins, *Tursiops truncatus*. *Zoo. Biol.* **10**, 451-456.
- Chivers, S. J. and M. D. Scott. (2002). Tagging and tracking of *Stenella* spp. during the 2001 Chase Encirclement Stress Studies Cruise. Administrative Report No. LJ-02-33, NMFS, Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, CA 92037.
- Curry, B. (1999). Stress in Mammals: the potential influence of fishery-induced stress on dolphins in the eastern tropical Pacific Ocean. *NOAA-TM-NMFS-SWFSC-260* **260**, 1-121.
- Dearoff, J., McLellan, W., Dillaman, R., Frierson, D. and Pabst, D. (2000). Precocial Development of Axial Locomotor Muscle in Bottlenose Dolphins (*Tursiops truncatus*). *Journal of Morphology* **244**, 203-215.
- Dickinson, S. (1929). The efficiency of bicycle pedaling, as affected by speed and load. *J. Physiol. London* **76**, 242-255.
- Dolar, M., Suarez, P., Ponganis, P. and Kooyman, G. (1999). Myoglobin in Pelagic Small Cetaceans. *Journal of Experimental Biology* **202**, 227-236.
- Donahue, M. A., B. L. Taylor and S. B. Reilly. (2000). IDCPA research program chase-recapture experiment consultation, Southwest Fisheries Science Center, La Jolla, California, 25-26 April 2000. Administrative Report No. LJ-00-15, NMFS, Southwest Fisheries Science Center, 8604 La Jolla Shores Drive, La Jolla, CA 92037. 14 pp.
- Edwards, E. (1992). Energetics of associated tunas and dolphins in the eastern tropical Pacific Ocean: a basis for the bond. *Fish. Bull.* **90**, 678-690.
- Elliot, J. and Davison, W. (1975). Energy Equivalents of Oxygen Consumption in Animal Energetics. *Oecologia* **19**, 195-201.
- Fish, F. (1998). Comparative Kinematics and Hydrodynamics of Odontocete Cetaceans: Morphological and Ecological Correlates with Swimming Performance. *Jl Exp. Biol.* **201**, 2867-2877.
- Fish, F. and Hui, C. (1991). Dolphin swimming - a review. *Mammal rev.* **21**, 181-195.

- Fish, F. and Rohr, J. (1999a). *Review of Dolphin Hydrodynamics and Swimming Performance*. San Deigo: SPAWAR SYSTEMS CENTER.
- Fish, F. and Rohr, J. (1999b). Maximum swimming speeds of dolphins: critical analysis of extraordinary performance (Abstract). In *13th Biennial Conference on the Biology of Marine Mammals*, pp. 57-57. Marine Mammal Society.
- Fish, F. (1993). Power Output and Propulsive Efficiency of swimming bottlenose dolphins (*Tursiops truncatus*). *Journal of Experimental Biology* **185**, 179-183.
- Fish, F. (1996). Transitions fro Drag-Based to Lift-based Propulsion in Mammalian Swimming. *Amer. Zool.* **36**, 628-641.
- Goldspink, G. (1988). *Muscle Energetics*. In *Mechanics and Energetics of Animal Locomotion*, (eds. Alexander R., and G. Goldspink. pp. 57-81.
- Gray, J. (1936). Studies in animal locomotion. IV. The propulsive powers of the dolphin. *J. Exp. Biol.* **13**, 192-199.
- Hampton, J. and Whittow, G. (1976). Body Temperature and Heat Exchange in the Hawaiian Spinner Dolphin, *Stenella longirostris* *Comp. Biochem. Physiol.* **55A**, 195-197.
- Hampton, J., Whittow, G., Szerkerczes, J. and Rutherford, S. (1971). Heat transfer and temperature in the Atlantic bottlenose dolphin (*Tursiops truncatus*). *Int. J. Biometeorol.* **15**, 247-253.
- Heithaus, M. (2001). Predator-prey and competitive interactions between sharks (order Selachii) and dolphins (suborder Odontoceti): a review. *J. Zool. London* **253**, 53-68.
- Hertel, H. (1969). Hydrodynamics of Swimming and Wave-riding Dolphins. In *The Biology of Marine Mammals*, (eds. H. Andersen), pp. 31-63. .
- Hoerner, S. (1965). *Fluid-Dynamic Drag*. Midland Park, NJ: Hoerner 148 Busted Drive.
- Hohn, A. and Hammond, P. (1985). Early postnatal growth of the spotted dolphin, *Stenella attenuata*, in the offshore eastern tropical Pacific. *Fish. Bull.* **83**, 553-566.
- Huesner, A. (1982). Energy metabolism and body size. Part I. Is the 0.75 mass exponent of Kleiber's equation a statistical artifact?. *Resp. Physiol.* **48**, 1-12.
- Hui, C. (1987). Power and speed of swimming dolphins. *J. Mamm.* **68**, 126-132.
- Karendeeva, O., Matisheva, S. and Shapunov, V. (1973). Features of external respiration in the Delphinidae. In *Morphology and ecology of marine mammals*, (eds. K. Chapskii and V. Salokov), pp. 196-206.
- Kelly, H. (1959). A two-body problem in the echelon-formation swimming of porpoise. In *Technical Note: 40606-1*, (eds. W. D. Division), pp. 1-7. China Lake, CA: U.S. Naval Ordnance Test Station.
- Lang, T. and Daybell, D. (1963). Porpoise performance tests in a seawater tank. Naval Ordnance Test Sta, China Lake, CA. *NAVWEPS Rept. 8060/NOTS Tech. Publ. 3063*.
- Lang, T. and Pryor, K. (1966). Hydrodynamic performance of Porpoises (*Stenella attenuata*). *Science* **152**, 531-533.
- Lang, T. (1975). Speed, Power, and drag measurements of dolphins and porpoises. In *Swimming and Flying in Nature*, (eds. T. Wu, C. Brokaw et al.), pp. 553-572. New York: Plenum Press.
- Lavigne, D., Barcyard, W., Innes, S. and Oritsland, N. (1982). Pinniped Bioenergetics. In *Mammals in the Sea*, vol. 4 pp. 192-235. FAO Fish Ser. 5.
- Leatherwood, S. and Ljungblad, D. (1979). Nighttime swimming and diving behavior of a radio-tagged spotted dolphin, *Stenella attenuata*. *Cetology* **34**, 1-6.

- Magnuson, J. (1978). Locomotion by scombroid fishes; hydromechanics, morphology and behavior. In *Fish Physiology*, vol. 7 (eds. W. Hoar and D. Randall), pp. 240-313. .
- McBride, A. and Kritzler, H. (1951). Observations on pregnancy, parturition, and post-natal behavior in the bottlenose dolphin. *Journal of Mammology* **32**, 251-266.
- Myrick, A. and Perkins, P. (1995). Adrenocortical color darkness as indicators of continuous premortem stress in chased and purse-seined male dolphins. *Pathophysiology* **2**, 191-204.
- Nagy, K. (1987). Field metabolic rate and food requirement scaling in mammals and birds. *Ecological Monographs* **57**, 112-128.
- Noren, S., Lacave, G., Wells, R. and Williams, T. (2001). The Development of Blood Oxygen Stores in Bottlenose Dolphins (*Tursiops truncatus*): Implications for diving capacity and Maternal Behavior. *draft MS.*
- Norris, K. and Prescott, J. (1961). Observations on Pacific Cetaceans of Californian and Mexican Waters. *Univ. Calif. Publ. Zool.* **63**, 291-402.
- Council, N. N. (1992). *Dolphins and the Tuna Industry*. Washington, DC: National Academy Press.
- Perkins, P. and Edwards, E. (1999). Capture rate as a function of school size in pantropical spotted dolphins, *Stenella attenuata*, in the eastern tropical Pacific Ocean. *Fish. Bull.* **97**, 542-554.
- Perrin, W., Coe, J. and Zweifel, J. (1976). Growth and Reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific Ocean. *Fishery Bulletin* **74**, 229-269.
- Skrovan, R., Williams, T., Berry, P., Moore, P. and Davis, R. (1999). The diving physiology of bottlenose dolphins (*Tursiops truncatus*) II. Biomechanics and changes in bouyancy at depth. *J. Exp. Biol.* **202**, 2749-2761.
- Videler, J. and Kamermans, P. (1985). Differences between upstroke and downstroke in swimming dolphins. *Journal of Experimental Biology* **119**, 265-274.
- Videler, J. (1993). *Fish Swimming*. London, UK: Chapman and Hall.
- Vogel, S. (1981). *Life in moving fluids: the physical biology of flow*. Boston, MA: Willard Grant Press.
- Webb, P. (1975). Hydrodynamics and Energetics of Fish Propulsion. *Bull. Fish. Res. Bd. Can.* **190**, 1-158.
- Weihs, D. and Webb, P. (1983). Optimization of Locomotion. In *Fish Biomechanics*, (eds. P. Webb and D. Weihs), pp. 339-371. New York: Praeger Publishers.
- Williams, T., Friedl, W., Fong, M., Yamada, R., Sedivy, P. and Haun, J. (1992). Travel at low energetic cost by swimming and wave-riding bottlenose dolphins. *Nature* **355**, 821-823.
- Williams, T., Friedl, W. and Haun, J. (1993). The physiology of bottlenose dolphins (*Tursiops truncatus*): heart rate, metabolic rate and plasma lactate concentration during exercise. *J. Exp. Biol.* **179**, 31-46.
- Williams, T., Haun, J. and Friedl, W. (1999). The diving physiology of bottlenose dolphins (*Tursiops truncatus*) I. Balancing the demands of exercise forenergy conservation at depth. *J. Exp. Biol.* **202**, 2739-2748.
- Williams, T. (1999). The evolution of cost efficient swimming in marine mammals: limits to energetic optimization. *Phil. Trans.R.Soc.Lond. B* **354**, 193-201.

- Worthy, G., Innes, S., Braune, B. and Stewart, R. (1987). Rapid acclimation of cetaceans to an open-system respirometer. In *Marine Mammal Energetics*, (eds. A. Huntley, D. Costa et al.), pp. 115-126. .
- Yadzi, P., Kilian, A. and Culik, B. (1999). Energy expenditure of swimming bottlenose dolphins. *Marine Biology* **134**, 601-607.
- Yates, G. (1983). Hydrodynamics of body and caudal fin propulsion. In *Fish Biomechanics*, (eds. P. Webb and D. Weihs), pp. 177-213. New York, NY: Praeger Publishers.

Table 1. Dolphin Model Parameters. See text for formulas and rationale.

Dolphin #	Age	Total Len. (cm)	Wet Wt. (kg)	Wetted Maximum			Est'd	Est'd
				Surf.Area (cm ²)	Diameter (cm)	fineness ratio	Optimum Velocity (cm/sec)	24-hour Standard Metab. (calories)
1	new born	85	6.40	2700	13.5	6.30	121.8	4.90E+05
2	1 week	87	6.85	2832	13.8	6.29	122.9	5.13E+05
3	1 month	90	7.58	3036	14.3	6.28	124.6	5.49E+05
4	3 months	98	9.76	3615	15.7	6.24	128.9	6.50E+05
5	6 months	110	13.76	4581	17.7	6.20	135.0	8.18E+05
6	1 year	129	22.08	6351	21.0	6.14	143.9	1.12E+06
7	2 years	154	37.37	9131	25.4	6.07	154.5	1.60E+06
8	adult	190	69.73	14045	31.7	5.99	168.0	2.43E+06

Chase Velocities:

cm/sec	m/sec	knots
25	0.25	0.50
50	0.50	1.00
100	1.00	2.00
150	1.50	3.00
200	2.00	4.00
250	2.50	5.00
300	3.00	6.00
500	5.00	10.00
600	6.00	12.00
750	7.50	15.00

Chase Durations:

minutes
15
30
60

Table 2. Reported burst, maximum, and sustained speed of individuals and school of dolphins.

Burst: (< 10 seconds)

11 m/sec	2 sec	Lang 1975 53 kg <i>Stenella</i>
9.1 m/sec	leap	Rohr and Fish 2000 captive <i>Tursiops</i>
9.1 m/sec	leap	Pershin 1988 (in Rohr and Fish 2000) <i>Delphinus</i>
8.8 m/sec	1-2 sec	Rohr and Fish 2000 <i>Delphinus</i> individual
8.2 m/sec	1-3 sec	Rohr and Fish 2000 captive <i>Tursiops</i> (several)
8.2 m/sec	leap	Au et al. 1988 <i>Stenella</i> avg exit speed
8.3 m/sec	7.5 sec	Lang 1975 89 kg <i>Tursiops</i> top speed
8.2 m/sec	< 2 min	Au et al. 1988 ETP <i>Stenella</i> school
8.0 m/sec	1-3 sec	Rohr and Fish 2000 captive <i>Delphinus</i>
7.8 m/sec	2 sec	Lang 1975 91 kg <i>lag</i> accel
7.7-8.3 m/sec	2 sec	Lang and Pryor 1966 2 <i>Stenella</i> max speed
7.6 m/sec	7.5 sec	Lang 1975 89 kg <i>Tursiops</i> fasted non-glide run
7.3 m/sec	leap	Au and Weihs 1980 ETP <i>Stenella</i>
7.0 m/sec	10 sec	Lang 1975 89 kg <i>Tursiops</i> fasted nonglide run
6.7 m/sec	1.4 sec	Rohr and Fish 2000 <i>Delphinus</i> max escape speed (helo)
6.7 m/sec	1-3 sec	Rohr and Fish 2000 <i>Delphinus</i> individual avg. max speed
6.7 m/sec	1-3 sec	Au and Perryman 1982 <i>Stenella</i>
6.4 m/sec	13 sec	Lang 1975 89 kg <i>Tursiops</i> top speed
6.2 m/sec	burst	Leatherwood and Lunjblad 1979 tagged ETP <i>Stenella</i>
6.2 m/sec	1-3 sec	Rohr and Fish 2000 <i>Tursiops</i> avg. max.speed
5.7 m/sec	2.7 sec	Rohr and Fish 2000 <i>Tursiops</i> max. escape speed
5.3 m/sec	6.6 sec	Lang 1975 89 kg <i>Tursiops</i> max sustained speed
4.2 m/sec	1.34 sec	Rohr and Fish 2000 <i>Delphinus</i> school avg escape speed (helo)

Limited (maximum) sustained (1-10 min)

6.1 m/sec	50 sec	Lang 1975 89 kg <i>Tursiops</i> fastest non-glide run
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Prolonged Sustainable (10 minutes-hours)

2.6-4.4 m/sec	26-86 min	Au and Perryman 1982 ETP schools, avg. speed
3.4 m/sec	26-86 min	Au and Perryman 1982 ETP schools, avg .speed
3.3 m/sec	indefinetly	Leatherwood and Lunjblad 1979 ETP tagged <i>Stenella</i>
3.1 m/sec	indefinetely	Lang 1975 89 kg <i>Tursiops</i>
2.3 m/sec	days	Perrin et al. 1979 <i>Delphinus</i> radio track
1.6 m/sec	all day	Hui 1987
1.5-2.8 m/sec	15-146 hours	Chivers and Scott 2001 9 ETP tagged <i>Stenella</i>

Appendix A. Responses to CIE reviewers.

Prepared by Elizabeth F. Edwards:

Responses to Reviewer's Comments on CIE -S12 "Potential effects of chase and encirclement on behavior and energetics of spotted dolphin (*Stenella attenuata*) mother-calf pairs in the ETP" and CIE-S13 "Energetic Consequences of chase by tuna purse seiners for spotted dolphins in the ETP" both by Elizabeth F. Edwards.

1. Response to comments from De. Guise:

Pages 4-5: "Reviews...seem unrealistic in view of field observations that calves do remain with cows during chase and capture operations". Verbage has been added at to CIE-S12 various places in the manuscript pointing out that probability of separation of specific mother-calf pairs will be affected by behavioral and physical characteristics of the individuals involved as well as by characteristics of individual chases (i.e., speed and duration) .

Page 16: "interesting and relevant...but quite pessimistic...". The reviewer is incorrect in saying that aerial observations "concluded that cow-calf pairs are not usually separated during chases".. Aerial photographs show a few seconds of swimming sequence of a given school. Persistence of a calf with a cow outside of those few seconds has not been demonstrated. The comments summarized above address the issue the reviewer raises again here.

2. Response to comments from D. Martineau:

pg 24-25: reviewer requests more emphasis on importance of frequent suckling to support energy needs of very young calf. Comments to that effect added in sections pertaining to very young calves.

3. No comments received from G. Bossart.

4. No comments received from R. Ortiz.

5. Response to comments received from J. Mann:

pg 8: review of CIE-12: reviewer comments that "some of the cited literature needs to reviewed more carefully". Review of references identified numerous instances of citations to a 1999 paper confused with a 1997 paper. These have been corrected. No other suggestions for corrections were made for this paper.

pg 9: review of CIE-13: The only direct suggestion for additional work appears in paragraph 2, recommending assessment of the likelihood that calves older than three months of age might still draft during times of stress. This cannot be determined from the existing literature, but would require either collection of new data, or possibly, examination of existing aerial photographs of ETP dolphin schools evading vessels and/or helicopters in the ETP. However, aerial photographs tend to capture only a few seconds in the swimming history of school, so the persistence of drafting by older calves probably couldn't be established from those data.